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STUDIES CONCERNING THE EVOLUTIONARY STATUS OF POLYCOTYLEDONY

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The question which condition is more primitive, polycotyledony or dicotyledony, has been very widely discussed and is a very old subject in botanical literature. It is generally believed that one of these has been derived from the other, and for more than seventy years botanical opinion has been divided on the question. On the basis of anatomy, Duchartre, in 1848, supported the thesis which had been previously announced, that polycotyledony has been derived from dicotyledony, but this view was not accepted by Sachs in his text-book (1882). Masters in 1891 supported the views of Sachs, and Dangeard supported the older view of Duchartre. More recently, Hill and DeFraine (6), after the study of the vascular anatomy of many conifer seedlings, also reached the conclusion that polycotyledony has been derived from dicotyledony by a splitting of the cotyledons.

Hill and DeFraine find that in most instances there is a single vascular strand in the cotyledon. They classify as whole-cotyledons those in which this strand undergoes bifurcation accompanied by a rotation of the xylem to bring the protoxylem in the exarch position as it forms a single root pole; as half-cotyledons those in which the strands from two cotyledons combine during transition to form one root pole; and as subsidiary-cotyledons those in which the strand fuses with another above the transition region. The existence of intermediate stages leads these authors to infer that "a subsidiary seed-leaf may, in the course of events, be promoted, as it were, to the rank of a half-cotyledon; while a half-seed-leaf may be raised to the dignity of a whole-cotyledon." In addition to this, they find that occasionally leaves from the plumule may become displaced and added to the cotyledonary node.

The argument of Hill and DeFraine rests further upon the existence of cotyledons with double strands, partially divided cotyledons, and numerous similar abnormalities. The theory is more plausible when applied to the Taxineae, Podocarpineae, and other forms with few cotyledons, but becomes very difficult to explain for the more extremely polycotyledonous Abietineae. While these authors make use of the external anatomy in their hypothesis, they give us no explanation for the origin of the cotyledonary tubes which they found in many instances among twenty species—nearly one third of the number investigated.

On the other hand, assuming that when two cotyledons fuse they form double cotyledons, which later lose their double nature, and that the cot-

yledonary tubes are the direct result of the incomplete fusions, it is just as easy, on the basis of the anatomical facts presented by Hill and DeFraine, to pass from polycotyledony to dicotyledony as *vice versa*. In support of the view that polycotyledony is primitive, Sister Helen Angela (1) has prepared a series of diagrams based on vascular anatomy, which show all stages in a series of intergrading forms from the polycotyledonous to the dicotyledonous condition, in Coniferales as well as in Cycadales. But the evidence mustered by vascular anatomy or by the study of the occasional freaks in which the cotyledons seem to be partly divided, is merely proof that one condition has without doubt arisen from the other, and leaves us with no very positive clue as to which course evolution has been taking—which condition has actually given rise to the other.

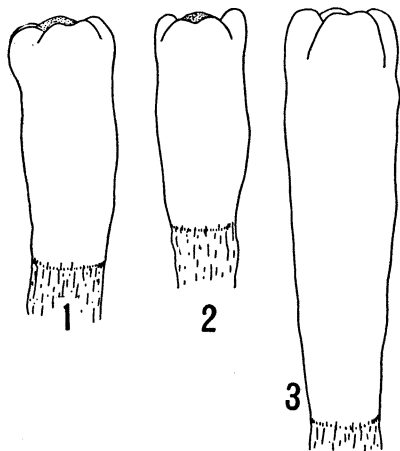
The study of fossil material has frequently furnished us with a definite record of the past history of a group. The fact that the embryos that have thus far been found in the most primitive gymnosperm seeds, those of the Bennettiales, are dicotyledonous has led to a rather widespread impression that geological proof establishes dicotyledony as the more primitive condition. On the other hand, it is now well known that the cycad line, of which the Bennettiales are the Mesozoic representatives, has been distinct from the conifer line since Paleozoic time. The Cordaitales were probably the ancestors of the whole conifer line which includes Ginkgoales as well as Coniferales. The cycad line, on the other hand, has been derived from the Cycadofilicales which also existed in Carboniferous time along with the Cordaitales, and these two phylogenetic lines of seed plants have been distinct from each other since very early times. Thus the dicotyledonous embryos of the Bennettiales do not represent the ancestral condition from which the conifers were derived, and we have no knowledge of the ancient conifer embryos from a study of fossil material. Coulter and Chamberlain (5), who do not accept the conclusions of Hill and DeFraine as final but favor the opposite view, point out that "probably our oldest group of Coniferales, older even than the Cycadales and Bennettiales with which we are acquainted, is the extreme illustration of polycotyledony, while the youngest of the Coniferales are dicotyledonous or nearly so." Until some paleobotanist describes embryo-bearing seeds of the most ancient conifers or Cordaitales, we shall need to look to our living material for our information, or content ourselves with a philosophical discussion of the question.

INVESTIGATION

This paper is the result of a study of the ontogeny of the cotyledons in various living species of conifers, in the hope that this evidence may reveal modern evolutionary tendencies and afford a safe criterion from which to determine in what direction this particular evolution of the cotyledons has been proceeding. When such evidence is not taken from a single isolated

species, but is found among representatives of different genera taken more or less at random and is in harmony with all the known facts, it establishes a safe morphological basis for conclusions.

The cotyledons develop in the other conifers in practically the same way as the writer has described for *Pinus* (2). As pointed out there, the stem tip primordium appears before the primordia of the cotyledons. It consists of a small protuberance at the apex of the dome which crowns the cylindrical cell mass of the undifferentiated embryo. Meanwhile, the whole embryo mass enlarges, and soon a circle of cotyledon primordia appear very nearly simultaneously, surrounding the stem tip. These primordia are little protuberances like the stem tip primordium and they soon elongate to form the cotyledons. They are separate and distinct from each other



FIGS. 1-3. Embryos of *Pinus Banksiana* which are occasionally found, showing cotyledonary fusion in the primordial stage. $\times 32$.

when they first appear, and their number is not constant but varies, much as does the number of cotyledons that are found in the matured embryo.

The primordia are formed long before there are any vascular strands. The latter are formed only some time after the cotyledons have begun to elongate. Therefore, evidence based on the origin of the primordia and of the cotyledons from these primordia has much greater morphological value than the study of the later appearing vascular structures, and has in addition the advantage of being capable of showing a definite recapitulation of the more primitive condition.

The writer has published evidence of cotyledonary fusions in the primordial stage of *Pinus Banksiana* (2). This species has a small number of cotyledons, ranging between three and six, the usual number being four. Here the number of primordia is sometimes greater than the number of cotyledons, and a number of instances were found which showed various

stages in the fusion of two cotyledon primordia to form single broad cotyledons, some of which are shown in figures 1, 2, and 3. In this species, the fusion is not always complete until after the cotyledons have begun to elongate, thus making its recognition as a process of fusion very certain.

Since this work on the pine embryo, the writer has been studying the embryos of a number of other conifers. Several species among other genera were found in which the cotyledons fuse in the primordial stages much as they do in *Pinus*, while still others were studied in which this performance has been completely eliminated from their ontogeny. However, no instances were found in which a small number of cotyledon primordia gave rise to a larger number of cotyledons.

Another good example of cotyledonary fusion may be found in *Picea mariana*. The material used in this study was sent to the Hull Botanical Laboratory from northern Wisconsin (Oneida County) about the first of August 1917. Through the kindness of Dr. George D. Fuller, the writer secured a number of cones from this collection. The specimen included the upper three feet of a black spruce tree unusually well laden with cones. Only one collection was available, and when the seeds proved to contain embryos in the cotyledon primordia stage, several hundred of them were dissected out under a binocular dissecting microscope and preserved in formalin-alcohol.

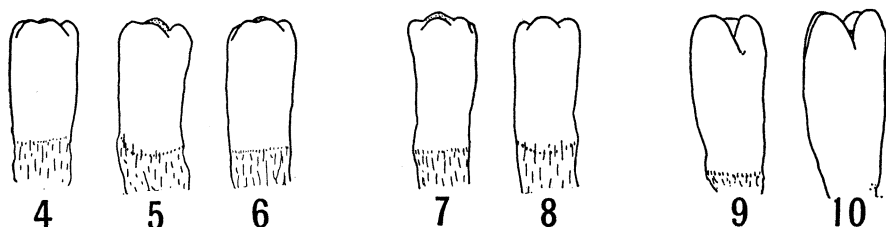
The drawings were made under the low power of a compound microscope with an Abbe camera lucida. Figures 1-3 and figures 24 and 25 are from stained permanent preparations; all of the remaining figures were made from the unstained embryos. In the figures, the stem tip primordium was shaded slightly so that it might be easily distinguished from the primordia of the cotyledons. The embryos are turned with their stem tips up because they are more easily handled in this position under the binocular dissecting microscope, the suspensor furnishing a convenient means of tilting, turning them over, and otherwise handling them without injuring their tips.

From the first, the writer was impressed by the large number of instances in which the sinus between two adjoining primordia seemed to be disappearing, resulting in a single broad cotyledon. By reference to the accompanying figures 4, 5, and 6, it will be noted that these primordia fuse very early, before there is any well marked elongation of the cotyledons. In many cases this fusion was so striking that it could easily be noticed, but in others it was less marked. To see these primordia distinctly, it was nearly always necessary to study the contour of the embryos as they were held in a slanting position and turned on their long axis with the apex pointing away from the observer. This avoids confusing the stem tip with the cotyledons, and makes young and obscure cases appear more distinct.

The writer realized that some of his readers would be inclined to take exception to conclusions based alone on appearances, as shown by the drawings of these embryos. Figures 4 and 6 might be looked upon as showing

broad primordia in a state of division, since in this species the fusion occurs before the cotyledons begin to elongate and is therefore much more rapid than in *Pinus Banksiana*. In the latter case, where the period of fusion usually lasts longer, this error of a reversed interpretation could not so easily be made. Furthermore, the variations that occur in the cotyledon number make it more difficult to recognize either a fusion tendency or the opposite condition.

To prove that these are cotyledonary fusions in *Picea*, it is necessary to rely in part on the statistical method. If, on an average, the younger embryos can be shown to have a larger number of cotyledon primordia than



Picea Mariana. FIGS. 4-6 are from lot B showing double cotyledon primordia that are undergoing fusion. FIGS. 7-8, embryos from lot C with no fusing primordia. FIGS. 9-10, embryos from lot D with young cotyledons which have developed well beyond the fusion stages. $\times 32$.

the average number of cotyledons in the older embryos, then there is unquestionably a reduction in their number, and the double primordia are in the act of fusion. If, on the other hand, the older embryos have a greater number of cotyledons than the number of primordia, or, counting these double primordia as two, if the resulting cotyledons are of the same average number as the primordia, then these double primordia must be cases of splitting cotyledons.

Sufficient variation in size was found between the youngest and the oldest embryos to make possible such a study, though they were all secured in one collection and dissected out within an interval of only five days, during which the material was kept living, though probably not growing as vigorously as if still attached to the tree. Unfortunately, other collections from the same tree were not possible after an interval of several weeks, for this would very much have simplified the task of studying them by this method. However, the facts were well shown even though based on this one collection of material, because there was considerable difference in size between the youngest and oldest embryos that were obtained.

By studying the embryos in a watchglass with a binocular dissecting microscope, examining them one at a time from all sides, they were divided into four lots. The embryos of lot A included all that were smaller than any of the figures shown; embryos too small to be considered because their primordia had either not appeared or were not distinct enough to be counted

with certainty; lot B, embryos like figures 4, 5, 6, and 10, in which there were evidences of either fusing or splitting cotyledons in the primordia stage; lot C, embryos of the same age as B, but showing no evidence of fusion by the grouping of their primordia; lot D, the oldest embryos, all older than B or C, in which, although the cotyledons were not fully developed, they were undoubtedly beyond the critical stages when fusions were found to occur. Figures 7, 8, 21, and 22 are from lot C and figures 9 and 10 from lot D.

The table below summarizes the result of this study. In lot B, all the primordial lobes were counted, even though in some instances they had practically fused with a neighbor, but broad cotyledon primordia which had no double tip were regarded as single primordia.

TABLE I. *The distribution of the cotyledons and cotyledon primordia in Picea mariana*

Cotyledons or Primordia, Number	Lot B, 23 Embryos, Frequency	Lot C, 83 Embryos, Frequency	Lot D, 63 Embryos, Frequency
3	0	9	5
4	6	53	42
5	18	20	15
6	4	1	1
Total primordia or cotyledons	138	345	264
Average primordia or cotyledons	4.93 \pm .39	4.16 \pm .41	4.17 \pm .39
Standard deviation (σ)59	.61	.58

Since lot D represents a late stage, and lots B and C represent an early stage, the averages of the number of cotyledons show that there is a reduction in the cotyledon number in the course of their development. Of course, this indicates that the double cotyledon primordia of the embryos in lot B are fusing.

It will be seen that if these were not fusing cotyledons, but in the course of separation, then the oldest group, lot D, might be expected to have an average of about 4.93 cotyledons, the average of lot B, or even more. The assumption that the embryos which were selected for lot C were not undergoing a fusion of their cotyledons was probably correct, since their average number of primordia, 4.16, agrees very closely with 4.17, the average number of cotyledons in lot D. However, lot B had an average of 0.76 cotyledons too many per embryo to agree with the number found in lot D.

A more careful analysis of the embryos of lot B showed that they could be classified in five categories, according to the number of primordia and the manner in which these were appearing to unite in forming cotyledons. On the twenty-eight embryos of the lot, forty-five double primordia were found, which ranged from such cases as were noticeable only when the embryos were held in a certain position, to others in which the fusion was nearly complete and the upper edge of the young cotyledon was only slightly retuse. The diagram of figure 6a illustrates the characters of the five gen-

eral categories, and the figures at the side indicate the number of embryos falling within each group.

It is to be expected that when the appearance of fusion is not very marked, as in many of the instances that were included in lot B, these double primordia will not all fuse to form single broad cotyledons. Many of them will form two distinct cotyledons in spite of the fact that they appeared to be fusing at an early stage.

If we may assume that twenty-eight fusions will occur, an average of one fusion for every embryo in lot B, then the average number of cotyledons

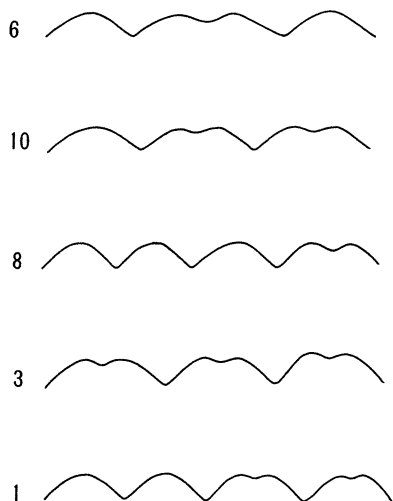


FIG. 6a. Diagrams illustrating the character of the five categories into which the embryos of *Picea mariana* (Lot B) were subdivided. The figures to the left indicate the number of embryos in each group.

produced in lots B and C combined will be 4.10, which is still quite close to the value 4.17, the average of lot D.

A study of *Larix europaea* gave very similar results. The material was secured at Dundee, Illinois, during the latter part of July 1917. The cones had been poorly pollinated and very few good seeds were found in each cone. The quantity of material was thus quite limited but included material from two collections gathered about a week apart. The embryos are only slightly larger than those of *Picea* in the cotyledon primordia stage, as is shown in figure 19.

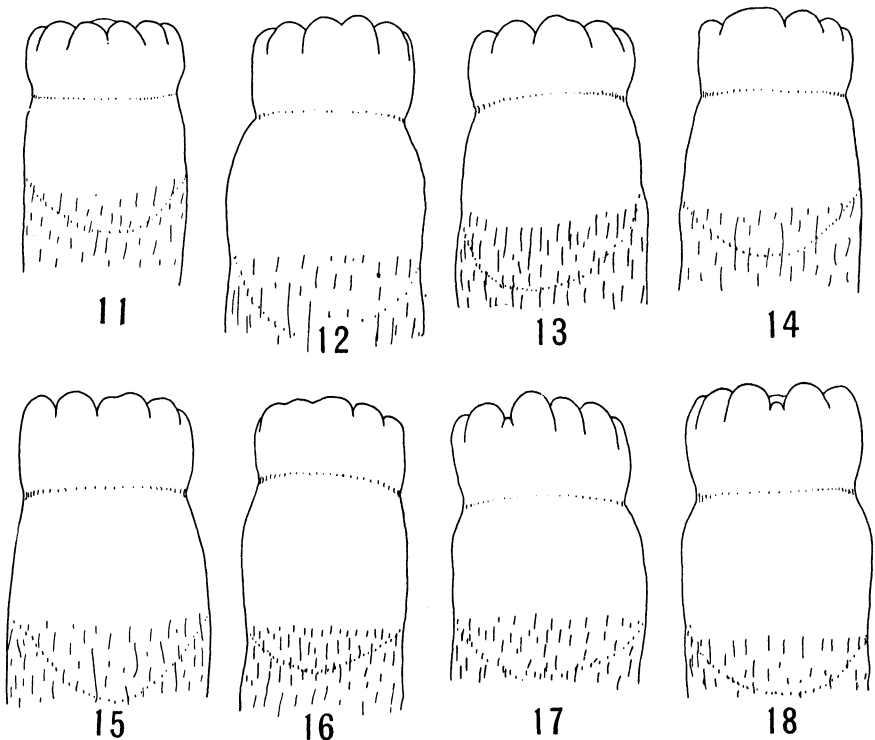
The embryos were separated into lots in the same way as those of *Picea*, and the results are tabulated below. It is significant that the average number of primordia in lot C agrees quite closely with the cotyledon average found in lot D, and that lot B has in this case an average of 0.55 primordia in excess of the number of cotyledons that it may be expected to produce, based on a comparison with lot D. However, considering the small num-

ber of cases that were observed, the conclusion that the cotyledons undergo a fusion in *Larix europaea*, while justified, is by no means so well established as is a similar conclusion in the case of *Picea*.

TABLE II. *The distribution of the cotyledons and cotyledon primordia in Larix europaea*

Cotyledons or Primordia, Number	Lot B, 6 Embryos, Frequency	Lot C, 10 Embryos, Frequency	Lot D, 34 Embryos, Frequency
5	1	3	11
6	2	7	20
7	3	0	3
Total primordia or cotyledons	38	57	196
Average primordia or cotyledons	$6.33 \pm .49$	$5.70 \pm .31$	$5.76 \pm .39$
Standard deviation (σ)74	.46	.59

Cedrus is another genus which was found to show fusing cotyledons. Through the kindness of Dr. E. J. Kraus, material of *Cedrus Libani* was sent to Texas from one of the trees growing on the Agricultural College grounds at Corvallis, Oregon. The cones were dissected (July 26, 1918) and were



Cedrus Libani. FIG. 11, an ordinary embryo without fusing primordia, or before any fusions may be seen. FIGS. 12, 13, and 15 show stages in the fusion of two cotyledon primordia. FIG. 14 has a broad cotyledon which has no doubt resulted from a fusion of two primordia. FIG. 16 shows three primordia fusing. FIGS. 17 and 18 show reduction of cotyledon number when primordia become aborted. $\times 32$.

found to contain embryos in the cotyledon-forming stages. There was again a great scarcity of good seeds in the cones, a condition which is due to poor pollination and is almost always met with when a species is cultivated out of its native region. That this species should show fusing cotyledons came as a surprise, because there were found to be from seven to twelve cotyledons (average about nine), and the writer had been expecting to find cotyledonary fusions among species with a small number of cotyledons.

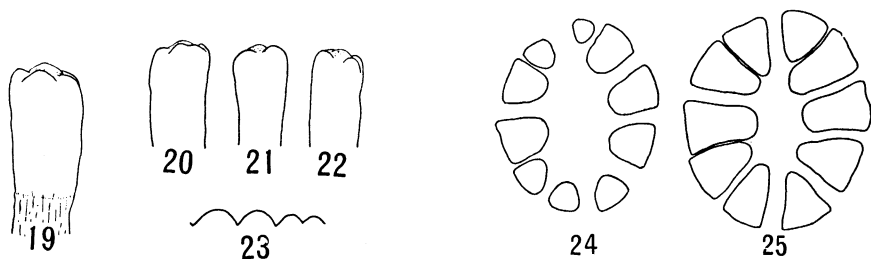


FIG. 19. *Larix* embryo from lot C showing a very slight inequality in the first appearance of the primordia. $\times 32$. FIGS. 20-22, embryos of *Picea mariana* showing a similar slight difference in the origin of the cotyledon primordia. FIG. 20 from lot B, FIGS. 21 and 22 from lot C. $\times 32$. FIG. 23, a diagram illustrating the manner in which cotyledon primordia frequently appear when unequally developed, suggesting that they are essentially spiral.

FIG. 24. Section near the tip of the cotyledons of a fully developed embryo of *Pinus Laricio*, showing a bilateral grouping of the cotyledons. FIG. 25, a similar section taken lower down on the same embryo.

The fusions of the primordia are gradual and so plainly seen that in this case, as in *Pinus Banksiana*, the statistical method is not necessary to convince one of what is taking place. Figure 11 shows an ordinary embryo with cotyledon primordia surrounding the primordium of the stem tip (shaded), and figures 12-16 show a number of typical cases with the fusing cotyledons. Out of twenty-five embryos in cotyledon primordia stages, eight such cotyledons were found which showed that fusions were taking place. Figure 16 shows three primordia that are apparently fusing.

Cedrus has two methods by which its cotyledons are reduced in number. One of these is fusion, and the other is the abortion of primordia as shown in figures 17 and 18. Two instances of this kind were found and are here figured, but in embryos much older than these this vestige would be overlooked, if it could be found at all.

An interesting fact which can be observed in many pine embryos is the tendency to become bilateral. The cotyledons frequently develop in two groups, and this is well shown in figure 24 which is drawn from a cross section near the tip of the cotyledons of an embryo of *Pinus Laricio*. As shown by figure 25, a section taken lower down on the same embryo, this arrangement of the cotyledons in two bilateral groups is noteworthy. It

is clear that if wholesale fusions should occur here it would probably result in dicotyledony or in a two-lipped cotyledonary tube. This tendency for the cotyledons to develop in two groups may be found in *Pinus Laricio*, *P. Banksiana*, *P. edule*, *P. Sabiniana*, and doubtless in many other species. It is not usually found in *P. Strobus*.

In *Abies balsamea*, *Juniperus commune*, and *Thuja occidentalis*, no evidences of cotyledonary fusions were found. The cotyledonary number is nearly fixed in these species, being usually four and occasionally five in *Abies balsamea*, and usually two, sometimes three, in *Thuja* and *Juniperus*. Not more than several dozen embryos of each of these species were examined in the cotyledon-forming stage, and these all with negative results.

Abies balsamea has a well developed sinus at the tip of each cotyledon, which makes the cotyledon appear strongly retuse. This character is developed after the cotyledons have begun to elongate, and is not due to fusing primordia as one might suspect in the light of the foregoing studies, after examining the cotyledons in any but the earliest stages of their development.

In his work on *Pinus*, the writer reported that the cotyledon primordia are usually simultaneous in their origin, but exceptions to this were found in which the primordia on one side appeared slightly before those on the opposite side. This tendency has been observed in *Pinus*, *Larix* (see fig. 19), *Picea* (see figs. 20-22), and occasionally in *Cedrus*, but the difference between the first and last primordia that appear is never very great. The primordia appear so nearly at the same time that on most of the embryos this feature is entirely overlooked. Figure 23 shows diagrammatically this slight difference in the size of the primordia on the same embryo in an extreme case, and this is quite frequently found in *Picea mariana*. It suggests that the cotyledons are essentially spiral in their origin, that they have become cyclic from a previous spiral condition.

Sometimes a zygomorphic tendency becomes evident some time after the primordia have appeared and the cotyledons have begun to elongate. The most extreme case of this kind was reported in a half-grown embryo of *Pinus Laricio* (2), and *Picea* showed several less marked examples. This zygomorphy which comes on some time after the primordia have appeared is not to be confused with the slight difference in the appearance of the primordia themselves, mentioned above.

The tendency toward spiral development exhibited by these cotyledon primordia suggested the idea that this may have been the more primitive condition, and made it seem desirable to know more definitely the condition of the first leaves of the plumule just above the cotyledons. An examination of the seedlings of several Abietineae shows that though the cotyledons are cyclic, their first simple leaves are arranged spirally, the condition which is well known for the older branches. The following seedlings were inspected: *Abies concolor*, *Pinus Strobus*, *Pinus Laricio*, *Pinus Banksiana*,

Pinus edule, *Pinus ponderosa*, *Pinus Sabiniana*, *Picea excelsa*, *Larix europaea* and *Pseudotsuga taxifolia*. It is in the upper axils of these spirally arranged simple leaves that the first needle-bearing branches appear toward the close of the first season's growth, and the older branches have the homologues of these simple leaves in the form of scales that likewise subtend the spur shoots.

DISCUSSION

The cotyledon primordia frequently fuse in *Pinus Banksiana* and *Cedrus Libani*, and this fact is so evident that it is not open to question, for here the process of fusion, when it occurs, is prolonged into the early stages of cotyledon elongation. The situation in *Picea* and *Larix* is not so simple, because the fusions of the primordia occur more suddenly, before the cotyledons elongate, making it necessary to employ the statistical method.

The appearance of a larger number of primordia than cotyledons is apparently a recapitulation of a feature in the phylogeny of the conifers, and since the examples chosen for study were selected from several different genera of the Abietineae, it indicates that the fusion tendency is quite general in this group. Occasionally the process expresses itself in other ways than by fusions, for a primordium sometimes becomes aborted in *Cedrus Libani*. It should be remembered that though some species failed to show fusions, no ontogenetic evidence of a splitting of cotyledons has been found in any species.

Recapitulation in external anatomy has long been recognized in the seedling stages of the conifers, such as *Thuja*, *Phyllocladus*, *Ginkgo*, etc. Jeffrey, in his recent work (8), cites numerous internal anatomical features which show recapitulation in the seedling stages. It is, therefore, not surprising that recapitulation should be found in the stages of the embryo before the seeds are shed. When the embryos are still enclosed within the seeds they are affected far less by the external conditions which bring about diversity. The writer has also demonstrated instances of recapitulation in the early embryos of the pine by finding that an apical cell of the pteridophyte type persists until an embryo mass of several hundred cells has been formed. Recapitulation has therefore been found in stages earlier as well as later than this cotyledon stage, and it is only to be expected that the cotyledon primordia should be found to show well marked tendencies to fuse if this is the manner in which dicotyledony has arisen.

The number of cotyledons in many species of gymnosperms is quite variable, and this variation has had a tendency to obscure any evidences of recapitulation. A fact which is significant in this connection is the well recognized tendency for a primitive or genetic form to show varying characters. A familiar illustration of this is shown in the number of petals, stamens, or carpels found in the Ranunculaceae, which belong to one of the lowest orders of the Archichlamydeae. Here the flower parts are spiral or

indefinite, and even when they become cyclic in the Ranales they are subject to fluctuation. It is easy to find a buttercup with extra petals, but it is seldom that the flower of a Phlox or a bluebell will show variations from the regular floral formula. Therefore it is very reasonable to regard this variation in the cotyledon number as an earmark of the low genetic position of the pines among the Coniferales.

This view falls in line with recent paleobotanical investigations which show that *Pinus* and the earlier form *Prepinus* are historically the most ancient conifers, also with the primitive position assigned to *Pinus* by the writer on the basis of its embryogeny.

Again, turning to our comparison of the cotyledons with floral structures, it is noteworthy that when floral members are spiral, their number is subject to the widest variation. Cyclic parts do not fluctuate so much, but when the cyclic condition is only very recently established they are also subject to considerable variation. Similarly, if the cotyledons still retain traits that characterize the spiral arrangement, this would account for the variation in their number which may be found in different individuals of any species. The first simple leaves that appear above the cotyledons in the young seedlings are spiral, and this also suggests that the cotyledons, which are doubtless modified from the first of these simple leaves, were originally spiral but have become more or less cyclic. The appearance of primordia on one side of the embryo before they are visible on the other is therefore also a vestigial character and an evidence of the original spiral condition of the cotyledons. Figure 23 shows the condition of the cotyledon primordia of many embryos, which may be taken to suggest that they are essentially spiral in their origin. These three features, namely, the variation in the cotyledon number, the spiral arrangement of the first leaves, and the slight tendency for the cotyledon primordia to appear on one side earlier than on the other, constitute the basis for the conclusion that the cotyledons themselves have become cyclic from a primitive spiral condition. To this might perhaps be added the evidence from the occasional displaced plumular leaves which Hill and DeFraigne find added to the cotyledonary node.

It is further interesting to call attention to the close parallel which seems to exist between the evolution of the floral members in angiosperms and that of the cotyledons of the embryo. In the flower, we pass from indefinite polypetaly to definite numbers in the floral members, then to sympetaly, which results in the corolla tube; this becomes two-lipped and finally ligulate, aside from its many other variations. A similar evolution has probably taken place in the history of the cotyledons. Originally, the cotyledons may have been spiral, but when the seed habit became established they soon became cyclic, the polycotyledonous condition today; these reduced their number by fusions, or occasionally by such methods as abortion of primordia. In some forms fusions became more general, resulting in the cotyledonary tubes.

Dicotyledony may have been attained in more than one way. One of these would be by checking the growth of the cotyledonary tube in two places during its development, much as a strongly bilabiate corolla develops. Another method is by a fusion of the cotyledons in two groups. This is strongly suggested by the bilateral grouping of the cotyledons in *Pinus Laricio*, and doubtless the tendency for the cotyledons to fuse, acting in concert with the cause which brings about this bilateral symmetry, could produce dicotyledony from polycotyledony.

That cotyledonary tubes are frequently found among gymnosperms was brought out by the work of Hill and DeFraine. The recent work of Hutchinson (7) on *Keteleeria* also shows that this embryo has a well developed cotyledonary tube and at the same time only four cotyledons, a rather reduced number. The fact that cotyledonary tubes have been found in angiosperms connects these with the polycotyledonous gymnosperms. Coulter and Land (4) have shown in a recent investigation how monocotyledony has been derived from dicotyledony by a zygomorphic development of the cotyledonary zone of an embryo which has a cotyledonary tube in an early stage of its development.

The writer has expressed the opinion that the cotyledonary tube had its origin in cotyledonary fusions. This is further suggested by the fact that *Agapanthus* has two primordia on a cotyledonary tube while *Cyrtanthus* has four primordia (4), and no doubt these are still further examples of embryonic recapitulation of an ancestral character, therefore distinctly pointing to polycotyledony as the more primitive condition.

The account which Coulter (3) gives for grass embryos as well as the one for *Cyrtanthus* completes our analogy between embryo and corolla development, for these monocotyledonous embryos come to correspond to the unilabiate or ligulate corolla by becoming extremely zygomorphic.

SUMMARY AND CONCLUSIONS

The results of this investigation show that in a number of conifers fusions of the cotyledons occur during their embryonic development. It is significant that no evidences of splitting cotyledons were found in any species.

The larger number of primordia found in the species exhibiting fusion is a recapitulation of a more primitive condition in which a larger number of cotyledons existed.

The fusion of cotyledons has given rise to a reduced number of cotyledons and also to cotyledonary tubes in some species. The occurrence of cotyledonary tubes in gymnosperms and the retention of this feature in some angiosperm embryos points to polycotyledony as the primitive condition.

All the definitely known facts brought out by others, as well as the investigations of the writer, may be used to support the following conclusions:

The primitive gymnosperm embryo had numerous cotyledons, which were imperfectly cyclic and variable in number. These cyclic cotyledons were in all probability derived from spirally arranged leaves that became cyclic in the cotyledonary node. Cotyledonary fusions reduced the number of cotyledons and also produced cotyledonary tubes in many species. Dicotyledony was attained either by a general fusion of many cotyledons in two groups, or by an extremely bilabiate development of a cotyledonary tube; and monocotyledony is the result of a cotyledonary tube becoming unilabiate in the course of its development. The polycotyledonous condition is therefore primitive and the dicotyledonous one is derived.

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